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Diversity and potential invasiveness of insects in agricultural landscapes of Wonosobo, Central Java, Indonesia

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[2]Laboratory of Animal Systematics, Faculty of Biology, Universitas Gadjah Mada. Jl. Teknika Selatan, Sleman 55281, Yogyakarta, Indonesia
[3]Biodiversity Research Group, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia

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Abstract. *Rahmadhani SE, Salsabila S, Andrianto R, Rosyida SH, Ainia Q, Dewangga A, Setyawan AD. 2025. Diversity and potential invasiveness of insects in agricultural landscapes of Wonosobo, Central Java, Indonesia. Asian J Agric 9: 663-670.* Altitude and microclimatic variation act as key ecological filters that shape species diversity, community structure, and invasion potential altitude, microclimate, and land-use intensity jointly structure insect communities in the agricultural landscapes of Wonosobo, Central Java, Indonesia. Surveys across lowland Karangsambung (621 masl), mid-elevation Blederan (969 masl), and highland Sembungan (2,056 masl) recorded 57 species from 31 families, revealing clear diversity gradients. Species richness and functional balance peaked at mid-elevation, where moderate temperatures and heterogeneous vegetation supported diverse herbivores, predators, and pollinators. Lowland sites retained high diversity driven by warm conditions and productive cropping systems. In contrast, highland assemblages were simplified and dominated by synanthropic Diptera (*Musca domestica*, *Leucostoma simplex*), reflecting harsh climatic filters and nutrient-enriched soils. NMDS-envfit analyses highlighted altitude, temperature, illumination, and wind as the main determinants of community structure. Invasiveness remained low overall, but disturbance-tolerant taxa increased with elevation. These findings emphasize the importance of vegetation heterogeneity, microclimate buffering, and biological control in sustaining ecological stability. As climate warming accelerates, mid-elevation agroecosystems may become critical resilience zones for conserving biodiversity and maintaining agricultural sustainability.

Keywords: Altitudinal gradient, agricultural landscape, Central Java, insect diversity, invasiveness

INTRODUCTION

Indonesia is recognized as one of the world's megadiverse countries, harboring approximately 10% of global flowering plants, 12% of mammals, 17% of birds, 25% of fish, and 15% of insects (CBD 2023). Insects comprise a substantial proportion of Indonesia's biodiversity, with around 250,000 species documented from an estimated 751,000 species globally. This exceptional richness is supported by Indonesia's stable tropical climate and complex ecological gradients, which provide a wide array of microhabitats (Andriani et al. 2017). Insects play critical roles in maintaining ecological balance as pollinators, decomposers, predators, and prey, thus influencing both natural and agricultural ecosystems (Alfianingsih et al. 2022). However, this biodiversity is under pressure from habitat conversion, pollution, and the introduction of non-native species that threaten the stability of local communities (Lukvitasari et al. 2021).

Insect diversity in agricultural landscapes is shaped by vegetation structure, crop type, and the intensity of land management practices (Fajarfika 2020). Areas with complex vegetation structures tend to support higher diversity due to the availability of multiple niches, while monoculture or intensively managed lands favor a few dominant taxa (Hidayat et al. 2022). In particular, elevation and temperature gradients are important environmental determinants that structure insect communities across tropical landscapes, influencing both diversity and functional composition. Higher altitudes generally harbor fewer species but more specialized taxa, whereas lowlands support abundant generalist species capable of adapting to variable microclimates. Such environmental heterogeneity in tropical mountains provides a valuable setting to study how insect assemblages respond to abiotic gradients, especially in agricultural ecosystems where natural and anthropogenic factors interact.

Invasive insect species represent an emerging ecological concern in Indonesia's agricultural regions. Invasive taxa can displace native species, disrupt pollination networks, and alter trophic interactions essential for crop productivity (Jupri et al. 2024). Their introduction may occur through human-mediated transport, climatic shifts, or habitat disturbances that weaken ecosystem resilience. For example, species such as *Musca domestica* and *Pantala flavescens* are known to exhibit broad ecological plasticity, enabling them to dominate disturbed or open habitats (Belioka and Achilias 2024; He et al. 2024). The success of these taxa in colonizing new environments depends on environmental suitability and the absence of natural enemies. Once established, invasive species may cause economic losses by damaging crops, spreading pathogens, and reducing populations of beneficial insects such as pollinators and natural predators (Sofian et al. 2023; Gul et al. 2024).

Recent studies in tropical Asia have shown that elevation-related changes in temperature, humidity, and vegetation structure can significantly influence the diversity and invasiveness of insect species. In mountainous agricultural areas, cooler temperatures and lower oxygen levels limit the distribution of many lowland insects, yet they may provide refuges for certain high-altitude or invasive species tolerant of harsh conditions (Adnan et al. 2024). Conversely, intensive farming practices, including pesticide use and land conversion, often simplify the habitat structure and reduce overall insect diversity (Permana et al. 2024). These conditions create ecological niches for opportunistic or cosmopolitan species to thrive, particularly those capable of rapid reproduction and adaptation. Understanding how environmental gradients influence community composition is therefore essential for predicting invasion risks and guiding sustainable pest management strategies.

Wonosobo District, located in the central highlands of Java, Indonesia, provides a unique setting for such ecological assessments. It is characterized by fertile volcanic soils derived from Mount Sindoro and Mount Sumbing and supports diverse cropping systems including potatoes, chilies, tomatoes, and rice (Gani et al. 2021; Findayani et al. 2024). The area's altitudinal range (600-2,100 meters above sea level/masl) produces strong microclimatic contrasts that shape the distribution and abundance of insect species. However, the expansion of agricultural land in these highlands has led to habitat simplification and the potential introduction of invasive species that threaten both biodiversity and agricultural productivity. Despite its ecological importance, insect community structure and invasiveness potential in Wonosobo's agricultural landscapes remain poorly documented.

Therefore, this study aimed to analyze the diversity, composition, and potential invasiveness of insects inhabiting agricultural landscapes in Wonosobo, Central Java, Indonesia. Specifically, it sought to (i) assess insect diversity and functional feeding groups across altitudinal gradients, (ii) identify species with potential invasive characteristics, and (iii) evaluate environmental factors influencing community structure. The findings are expected to support the development of ecologically based pest management strategies that maintain biodiversity while ensuring agricultural sustainability.

MATERIALS AND METHODS

Study area

Geographic and environmental setting of Wonosobo District

Wonosobo District in Central Java, Indonesia (7°11′-7°36′S; 109°43′-110°04′E) lies between Mount Sindoro and Mount Sumbing in the Dieng Plateau. Elevations range from 600-2,100 masl, with a tropical monsoon climate, annual rainfall of 2,500-3,000 mm, and temperatures decreasing from 25 °C in the lowlands to about 17 °C in the uplands (Gani et al. 2021). Andisol and inceptisol soils derived from volcanic ash support intensive horticulture, although steep-slope cultivation causes erosion and nutrient depletion, a pattern widely reported in volcanic highlands (Whitten et al. 1996). The district forms a mosaic of croplands, riparian strips, forest remnants, and grasslands, creating heterogeneous habitats that influence insect assemblages, consistent with landscape-biodiversity interactions in tropical agroecosystems (Tscharntke et al. 2005). This environmental complexity makes Wonosobo suitable for studying how altitudinal and microclimatic gradients shape insect diversity, a phenomenon widely observed in tropical mountain systems (Rahbek 1995; Hodkinson 2005).

Site descriptions: Karangsambung, Blederan, and Sembungan

Fieldwork in October 2024 covered three agricultural sites representing low, mid, and high elevations (Figure 1). Karangsambung (621 masl) is a warm lowland near a river, dominated by corn, cassava, and rice cultivation. Blederan (969 masl) represents mid-elevation farmland with tomato, chili, and cabbage systems, characterized by moderate temperatures and relatively open canopies. Sembungan (2,056 masl), located near Telaga Cebong, has cool, humid conditions supporting potato and *Carica pubescens*. To confirm microclimatic distinctiveness, temperature, light intensity, wind speed, and altitude were tested using one-way ANOVA ($P < 0.05$). These differences provide a framework for interpreting site-specific patterns of herbivores such as *Dinoptera* sp., *Lema praeusta*, *Henosepilachna vigintioctopunctata*, and *Anomala dimidiata*, as well as predators such as *Cheilomenes sexmaculata*, *Coccinella septempunctata*, and *Paederus fuscipes*, and dipterans including *Leucostoma simplex*, *Morellia hortensia*, and *M. domestica*.

Altitudinal gradient and agricultural characteristics

The 621-2,056 masl gradient generates marked environmental transitions that influence vegetation and insect distribution. As shown in Table 1, temperature declines with elevation, whereas wind speed and light intensity increase, producing abiotic contrasts that shape insect abundance and composition. Lower elevations favor warm-adapted species, while the cooler uplands of Sembungan support taxa such as *L. simplex* and *M. domestica*, which tolerate humid, organic-rich environments. This vertical stratification aligns with ecological expectations of declining diversity but increased specialization at higher altitudes, as reported in global elevational biodiversity studies (Rahbek 1995; Hodkinson 2005). Agriculturally, the gradient reflects a shift from mixed lowland cropping systems to intensive upland horticulture, where reduced habitat heterogeneity may elevate pest risks, consistent with the agroecological intensification model (Perfecto and Vandermeer 2010) and its known effects on biodiversity and pest dynamics (Tscharntke et al. 2005). Figure 1 illustrates landscape variation across sites, emphasizing the importance of altitudinal patterns for sustainable pest management in highland agricultural systems.

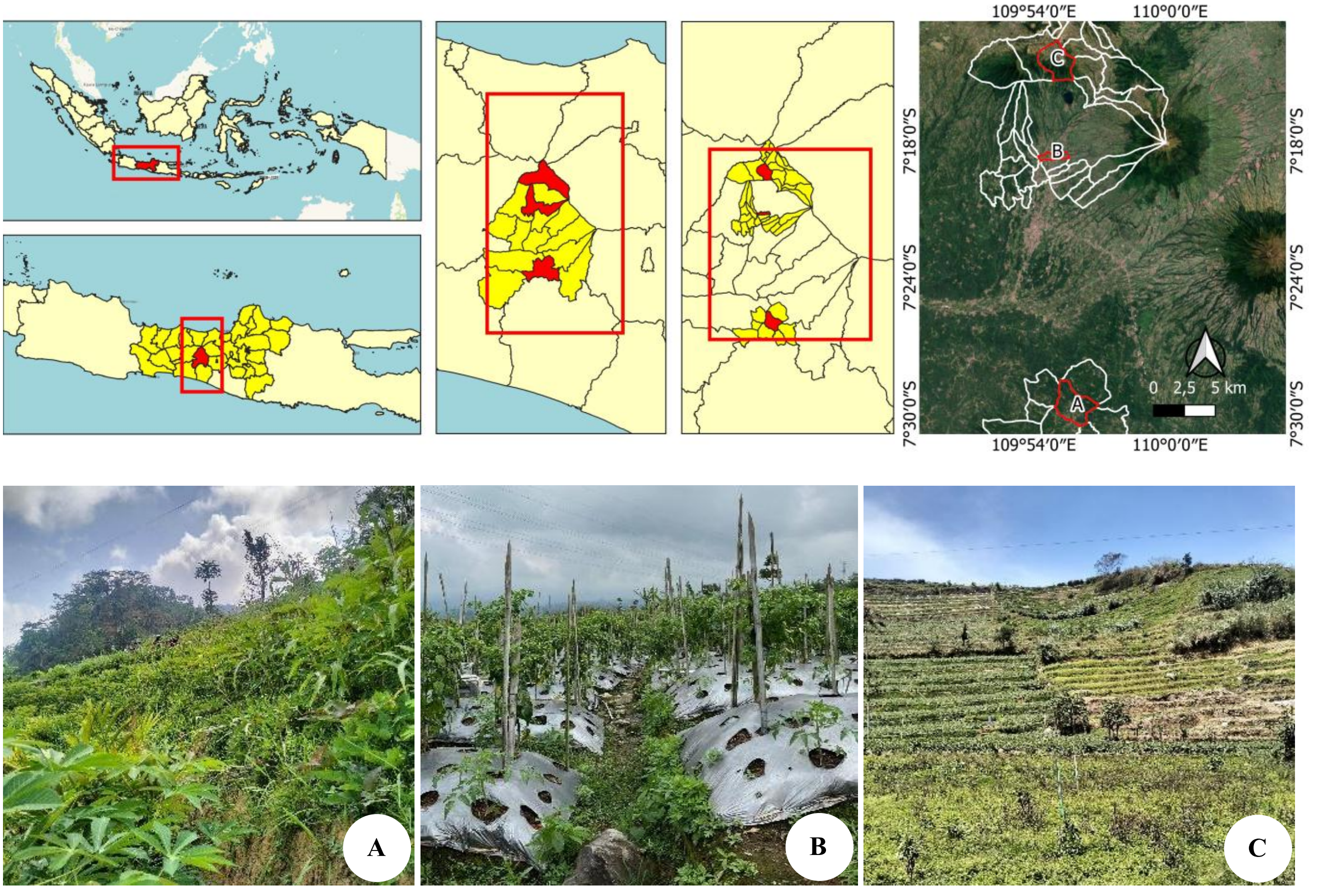


Figure 1. Locations of the three study sites in Agriculture landscape of Wonosobo, Central Java, Indonesia. A. Karangsambung (Site 1), B. Blederan (Site 2), and C. Sembungan (Site 3), Wonosobo, Central Java, Indonesia

Sampling design and data collection

Sampling was conducted in October 2024 at three agricultural sites—Karangsambung, Blederan, and Sembungan (Figure 1)—covering a clear altitudinal gradient from lowland to highland systems in Wonosobo District. A stratified-random sampling design was applied to represent ecological variation by elevation, crop type, and hydrology, ensuring both horizontal (land-use) and vertical (altitude) gradients were captured.

Sampling period and site selection criteria

Sampling coincided with the dry-wet transition, when crops were at their reproductive phase and insect activity typically peaks (Adnan et al. 2024). Sites were selected based on accessibility, minimal pesticide use for at least two weeks prior, and representativeness of local agricultural practices (Sofian et al. 2023). Each site encompassed 1 ha and was divided into ten randomly selected 5 × 5 m plots positioned away from field margins to minimize edge effects (Yanti et al. 2023). This approach ensured statistical independence and comparability across elevations.

Plot design and sampling methods

To maximize coverage of insect strata, three complementary methods were employed (Leksono 2017): (i) Sweep netting: Five-minute sweeps per plot using a 38-cm net for foliage and flowering insects. (ii) Aerial netting: Ten-minute surveys targeting fast-flying taxa (e.g., Odonata, Diptera) from 09:00 to 14:00. (iii) Handpicking: Manual collection of ground-dwelling species for five minutes per plot. All collections were done under clear weather, and specimens were immediately preserved in 70% ethanol.

Specimen labeling, preservation, and identification

Each specimen was labeled with site code (K, B, S), altitude, date, and plot number, then pinned or preserved in alcohol according to fragility. Identification followed morphological keys and databases (GBIF 2024; iNaturalist 2024; ITIS 2024). Questionable taxa were rechecked under a stereo microscope, and verified identifications were deposited as voucher specimens at the Department of Environmental Science, Universitas Sebelas Maret, Indonesia.

Environmental and microclimatic data

At each plot, temperature, light intensity, wind speed, and altitude were measured concurrently at 1.5 m height using calibrated instruments. Temperature was recorded with a digital thermometer, light with a lux meter, wind speed with an anemometer, and altitude with a GPS. These data characterized microclimatic variability influencing insect composition (Azhar et al. 2024).

Measurement protocol and data reliability

All measurements followed standardized procedures (Odum 1993; Redowan 2015) and were taken during morning-midday hours to represent diurnal insect activity. Instruments were recalibrated daily, and readings were replicated three times per plot. Statistical analysis confirmed significant microclimatic differences ($P < 0.05$) among sites, validating their representation of distinct altitudinal environments (Shah et al. 2025).

Integration with landscape context

The spatial distribution of the three study sites across the Wonosobo highlands, combined with representative agricultural landscapes, is shown in Figure 1. Lowland Karangsambung exhibits warm and moist conditions, mid-elevation Blederan reflects intermediate microclimates, and upland Sembungan is characterized by cooler temperatures and higher wind velocity. Integrating spatial layout with landscape characteristics in a single figure provides a clearer ecological context for interpreting how environmental gradients and land-use heterogeneity shape insect community composition and invasiveness potential in tropical highland agroecosystems.

Data analysis

Ecological indices

To assess the diversity structure of insect communities, several standard ecological indices were calculated following Shannon and Wiener (1949), Margalef (1958), Odum (1993) and Redowan (2015). These indices provide complementary information about community composition, species dominance, and evenness across the altitudinal gradient.

The Shannon-Wiener Diversity Index (H′) was used to estimate species diversity based on the proportion of individuals among taxa. The index is sensitive to both species richness and evenness, offering a balanced measure of diversity (Magurran 2004).

$$H\prime = -\sum_{i=1}^{S} \frac{n_i}{N} \ln \frac{n_i}{N}$$

Where n_i is the number of individuals in species i, N is the total number of individuals, and S is the total number of species recorded. The values were interpreted as low ($H' < 1$), moderate ($1 < H' < 3$), and high ($H' > 3$).

Simpson's Dominance Index (C) was computed to determine dominance patterns among species. Values close to 0 indicate low dominance (high diversity), while values near 1 suggest strong dominance by a few taxa (Odum 1993).

$$C = \sum_{i=1}^{S} \left(\frac{n_i}{N}\right)^2$$

Evenness (E) was determined using Pielou's Evenness Index to evaluate the uniformity of individual distribution among species. This index complements Shannon's diversity by showing whether assemblages are numerically balanced.

$$E = \frac{H\prime}{\ln S}$$

Values were categorized as low ($E < 0.3$), moderate ($0.3 < E < 0.6$), and high ($E > 0.6$).

Species richness (DMg) was calculated using Margalef's index, which accounts for the influence of rare species (Ludwig and Reynolds 1988). Integrating these indices allows for multi-dimensional interpretation of community structure across the altitudinal transect.

$$DMg = \frac{S-1}{\ln N}$$

According to Margalef (1958), values of $DMg < 3.5$ indicate low richness, 3.5-5.0 moderate richness, and >5.0 high richness.

Functional feeding group classification

All recorded insect species were classified into Functional Feeding Groups (FFG) based on their primary ecological roles—herbivores, predators, nectarivores, saprophages, detritivores, and omnivores. Classification followed the ecological framework of Sollai et al. (2024) and standard entomological references (Leksono 2017; Mashami et al. 2022), supported by species-level data from GBIF (2024), iNaturalist (2024) and ITIS (2024). Functional grouping reflects trophic contributions to agroecosystems and enables consistent comparison among sites. Similar approaches have been widely applied in tropical agricultural landscapes (Tscharntke et al. 2005; Kremen et al. 2007).

Assessment of invasiveness status

The invasiveness status of each species was evaluated using an integrative approach combining literature review and verification through authoritative databases, including the Global Biodiversity Information Facility (GBIF 2024), Integrated Taxonomic Information System (ITIS 2024), the CABI (2024), and regional Southeast Asian faunal checklists. Based on consolidated definitions from the IUCN-ISSG (2000), the invasion frameworks of Richardson et al. (2000), the Convention on Biological Diversity (CBD 2002) and Blackburn et al. (2011), all species were assigned to one of three ecological categories: Native, Invasive Alien Species (IAS), or potentially invasive.

Native species were defined as taxa with natural evolutionary origins within Indonesia or the broader Southeast Asian region. Invasive Alien Species (IAS) refers to non-native taxa that are established, self-sustaining, and known to cause ecological or agricultural impacts. Potentially invasive species included cosmopolitan, synanthropic, or naturalized taxa with broad ecological tolerance and the ability to persist in disturbed habitats, although not formally classified as invasive. Descriptors such as widespread Asian, naturalized, or synanthropic were retained in parentheses to provide additional biogeographical context without constituting separate categories.

Each classification was cross-validated using species traits (e.g., dispersal ability, reproductive potential, habitat breadth, and disturbance tolerance) and distributional evidence from regional literature. This streamlined categorization facilitates a clearer interpretation of invasion risk, community structure, and site-level vulnerability to non-native colonization. Classification was further validated using species traits and ecological information (Liebhold et al. 2012; Seebens et al. 2017).

Statistical analyses

Statistical analyses were conducted to assess spatial variation in environmental conditions and to evaluate differences in insect community structure across the three agricultural sites. Microclimatic variables (temperature, altitude, light intensity, and wind speed) were compared using one-way ANOVA followed by Tukey's HSD at $P < 0.05$ to determine pairwise differences among sites. Abundance data were transformed using $\log_{10}(x + 1)$ to reduce the influence of highly dominant taxa—particularly *M. domestica* and *L. simplex*—and to improve variance homogeneity before multivariate analyses (Quinn and Keough 2002).

A Bray-Curtis similarity matrix was constructed from the transformed abundance data to quantify compositional differences among sites. Community similarity patterns were visualized using Non-metric Multidimensional Scaling (NMDS), producing a stable two-dimensional ordination consistent with the clear separation of Sembungan reported in the Results. Principal Coordinates Analysis (PCoA) was used as a complementary ordination method to identify major gradients associated with high Dipteran abundance in upland habitats versus Orthoptera- and Hymenoptera-rich assemblages at lower elevations (Legendre and Legendre 2012).

Hierarchical clustering using UPGMA was performed to examine grouping patterns among sites, supporting the formation of a low-mid elevation cluster (Karangsambung + Blederan) and the distinct highland assemblage in Sembungan. Whittaker's beta diversity (β_W) was calculated from site-level species richness to quantify species turnover along the altitudinal gradient (Whittaker 1972; Anderson et al. 2011).

All statistical procedures were carried out using PAST 4.10 and R version 4.3.0. This integrated analytical framework—combining univariate tests, similarity-based ordination, and clustering—provides a robust basis for interpreting the strong environmental filtering and high-elevation specialization observed in the insect communities of the Wonosobo agricultural landscape.

RESULTS AND DISCUSSION

Physicochemical characteristics of study sites

Air temperature differed significantly among the three agricultural sites (Table 1). Karangsambung recorded the warmest conditions (24.6 ± 0.81°C), followed by Blederan (21.8 ± 1.24°C), while the highland site of Sembungan exhibited the lowest mean temperature (18.6 ± 0.40°C). This decline of approximately 6°C along the elevational gradient reflects the typical mountain lapse rate, where higher altitudes experience reduced atmospheric pressure and lower heat retention, creating distinct thermal niches that shape insect physiology, activity, and reproductive dynamics.

Wind velocity also varied significantly across sites ($P < 0.05$). Sembungan recorded the highest wind speed (6.60 ± 0.20 km h^{-1}), characteristic of its open upland terrain. In contrast, Blederan and Karangsambung showed lower wind speeds (5.72 ± 0.23 and 5.58 ± 0.17 km h^{-1}, respectively). Higher wind exposure in the highlands can influence dispersal of flying insects such as Odonata, while calmer conditions in lower elevations promote stable foraging activity among herbivores and pollinators.

Light intensity measured in lux exhibited strong site differences. Sembungan had the highest illumination (677.8 ± 18.77 lux), reflecting open, less-shaded highland agricultural landscapes. Karangsambung showed moderate illumination (307.8 ± 96.86 lux), whereas Blederan recorded the lowest levels (157.0 ± 30.43 lux). Such variation affects insect thermoregulation, flight behavior, and nectar/pollen foraging, with high-light environments favoring visually oriented taxa like Diptera and Odonata.

The altitudinal gradient across the study sites was pronounced and statistically significant ($P < 0.05$). Karangsambung lies at 621 ± 0.89 masl, Blederan at 969 ± 0.94 masl, and Sembungan at 2,056 ± 0.46 masl. This steep elevational transition shapes multiple interacting environmental drivers—including temperature decline, changes in wind exposure, and shifts in vegetation structure—that together influence insect community composition, resource availability, and habitat suitability.

Collectively, the three sites represent distinct microclimatic zones within the Wonosobo highlands. Karangsambung reflects warm, low-elevation agroecosystems; Blederan represents a temperate mid-elevation environment with moderate illumination; and Sembungan embodies cool, windy, high-elevation conditions with high light exposure. These contrasts, confirmed by one-way ANOVA (Table 1), underpin the observed differences in insect community structure and trophic dynamics across the altitudinal gradient.

Composition of insect assemblages

A total of 57 insect species representing 31 families and 9 orders were recorded across the three agricultural sites, comprising 692 individuals in total (Table 2). Species richness and abundance varied distinctly along the altitudinal gradient. Karangsambung (lowland, 621 masl) supported 25 species and 232 individuals, while Blederan (mid-elevation, 969 masl) exhibited the highest richness with 27 species and 183 individuals. Sembungan (highland, 2,056 masl) recorded lower richness (17 species) yet the highest abundance (277 individuals), indicating strong dominance by a few tolerant taxa.

Table 1. Physicochemical characteristics (x ± SE) of agricultural land in Wonosobo, Central Java, Indonesia

Characteristics	Unit	Karangsambung	Blederan	Sembungan	F-count	Significance
Air temperature	°C	24.6 ± 0.81 b	21.8 ± 1.24 ab	18.6 ± 0.40 a	42.37	$P < 0.05$
Wind speed	km h^{-1}	5.58 ± 0.17 a	5.72 ± 0.23 a	6.60 ± 0.20 b	8.91	$P < 0.05$
Luminous intensity	lux	307.8 ± 96.86 a	157.0 ± 30.43 a	677.8 ± 18.77 b	56.14	$P < 0.05$
Altitude	masl	621 ± 0.89 a	969 ± 0.94 b	2055.8 ± 0.46 c	219.53	$P < 0.05$

Note: Different superscript letters within a row indicate significant differences among sites according to one-way ANOVA followed by Tukey's HSD ($P < 0.05$)

The 57 recorded species were distributed across multiple insect orders dominated by Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera, and Trichoptera. Several families were represented by multiple species, including Chrysomelidae, Coccinellidae, Muscidae, Formicidae, Nymphalidae, Libellulidae, and Acrididae, reflecting the taxonomic diversity typical of tropical agricultural systems. Diptera, Hemiptera, and Orthoptera contributed substantially to highland and midland communities, while Hymenoptera and Odonata were prevalent in warmer lowland and mid-elevation sites.

Dominant taxa differed sharply among sites. In Karangsambung, the most abundant species was the omnivorous ant *Carebara diversa* (69 individuals), accompanied by herbivorous Orthoptera such as *Oxya japonica* and *Acrida cinerea*. Blederan exhibited no single overwhelmingly dominant species, but several taxa were notable for their higher abundances, including the predator *P. fuscipes* (7 individuals) and the dragonfly *Orthetrum sabina* (5 individuals). In contrast, Sembungan was characterized by extreme dominance of saprophagous Diptera—particularly the synanthropic *M. domestica* (82 individuals) and the disturbance-tolerant *L. simplex* (47 individuals)—indicative of cool, moist, and organic-rich highland conditions.

Spatial patterns revealed clear altitudinal structuring of insect assemblages. Lowland Karangsambung supported diverse herbivore-omnivore assemblages typical of mixed-crop agroecosystems. Mid-elevation Blederan exhibited the highest species richness and balanced trophic composition, likely driven by moderate microclimates and heterogeneous vegetation. Highland Sembungan, however, showed reduced richness but elevated individual abundance due to dominance by cold-tolerant, synanthropic Diptera associated with moist organic substrates near Telaga Cebong. This distribution pattern reflects strong environmental filtering, where temperature, moisture, and habitat structure shape the taxonomic and functional composition of insect communities across the Wonosobo landscape.

Functional feeding groups of insects

Across the 57 insect species recorded in the three agricultural sites of Wonosobo, six Functional Feeding Groups (FFGs) were identified, reflecting the trophic diversity of the assemblage. Herbivores were the dominant group, comprising 33 species (58%), followed by predators with 12 species (21%), detritivores with 7 species (12%), nectarivores with 3 species (5%), and smaller contributions from saprophages (2 species; 3%) and omnivores (2 species; 3%). This trophic composition indicates that herbivory is the primary ecological process shaping insect communities in the region's mixed-crop agroecosystems, with predation and decomposition functioning as secondary but essential pathways that support ecosystem stability.

The distribution of FFGs varied markedly across lowland, mid-elevation, and highland sites. Herbivores dominated the assemblages in Karangsambung and Blederan, where mixed vegetation and cultivated crops provide abundant foliage resources for Acrididae, Pentatomidae, and Lepidoptera. Predators, including dragonflies (Libellulidae), ants (Formicidae), and rove beetles, were more frequent at mid- to high elevations, reflecting the favorable microclimatic conditions—moderate to cool temperatures—required for active foraging. In contrast, Sembungan, the highland site at 2,056 masl, was heavily characterized by detritivores and saprophages, especially *L. simplex*, *M. domestica*, and Tipula javana, all of which thrive in cool, moist, organic-rich substrates. This concentration of decomposer taxa highlights the strong influence of altitude and moisture regime on trophic structuring.

The clear separation of trophic groups along the altitudinal gradient illustrates how environmental filtering shapes ecological roles within agricultural landscapes. Lowland and mid-elevation farms maintain functionally diverse, herbivore-driven assemblages, supporting herbivory regulation, pollination, and predator-prey interactions typical of productive agroecosystems. Highland communities, however, shift toward decomposition-based trophic pathways, driven by the dominance of saprophagous and detritivorous Diptera under cooler and wetter conditions. Despite turnover in species identities across elevations, the overall trophic structure remains balanced, indicating a resilient functional network capable of maintaining ecosystem processes under varying microclimatic conditions. Nevertheless, the presence of disturbance-tolerant, potentially invasive taxa—particularly in the highlands—suggests that future land-use intensification or climatic shifts could alter trophic dynamics and community stability.

Table 2. Terrestrial insect found in agriculture land of Wonosobo, Central Java, Indonesia

Order	Family	Species	Study site			Total	FFG*	Status
			Karang-sambung	**Blederan**	**Sembungan**			
Coleoptera	Cerambycidae	*Dinoptera* sp.	1	-	-	1	Herbivore	Native (genus-level, regional)
	Chrysomelidae	*Lema praeusta* (Fabricius, 1792)	1	1	-	2	Herbivore	Native
	Coccinellidae	*Cheilomenes sexmaculata* (Fabricius, 1781)	1	9	-	10	Predator	Native (widespread Asian)
		Coccinella septempunctata Linnaeus, 1758	-	-	1	1	Predator	Invasive Alien Species (alien beetle, widely established)
		Henosepilachna vigintioctopunctata (Fabricius, 1775)	-	8	-	8	Herbivore	Native
	Scarabaeidae	*Anomala dimidiata* (Hope, 1831)	-	-	2	2	Herbivore	Native
	Staphylinidae	*Paederus fuscipes* Curtis, 1826	-	7	-	7	Predator	Native (Old World widespread)
Dermaptera	Forficulidae	*Forficula auricularia* (Linnaeus, 1758)	-	4	-	4	Predator	Invasive Alien Species (cosmopolitan earwig)
Diptera	Lauxaniidae	*Leucostoma simplex* (Zetterstedt, 1838)	-	-	47	47	Detritivore	Potentially invasive (cosmopolitan, disturbance-tolerant)
	Muscidae	*Morellia hortensia* (Rondani, 1866)	-	-	5	5	Saprophage	Potentially invasive (regional synanthropic)
		Musca domestica (Linnaeus, 1758)	-	5	82	87	Saprophage	Potentially invasive (cosmopolitan synanthropic)
	Syrphidae	*Episyrphus trisectus* (Matsumura, 1917)	-	-	3	3	Nectarivore	Native
		Melanostoma scalare (Fabricius, 1794)	-	3	-	3	Nectarivore	Native (widespread Asian/Oriental)
	Tipulidae	*Tipula (Acutipula) javana* (Walker, 1860)	-	-	17	17	Detritivore	Native
Hemiptera	Cicadidae	*Platylomia radha* (Distant, 1881)	-	1	-	1	Herbivore	Native
	Coreidae	*Mictis longicornis* (Fabricius, 1798)	1	-	55	56	Herbivore	Native
		Physomerus grossipes (Fabricius, 1798)	2	-	-	2	Herbivore	Native
	Delphacidae	*Peregrinus maidis* (Ashmead, 1890)	33	20	-	53	Herbivore	Invasive Alien Species (invasive agricultural pest)
	Pentatomidae	*Eurydema pulchrum* (Westwood, 1837)	-	1	-	1	Herbivore	Native
Hymenoptera	Apidae	*Apis cerana* (Fabricius, 1793)	-	-	3	3	Nectarivore	Native
	Formicidae	*Carebara diversa* (Jerdon, 1851)	69	-	-	69	Omnivore	Native
		Odontoponera denticulata (Smith, 1858)	-	18	-	18	Predator	Native
		Polyrhachis illaudata (Walker, 1859)	6	2	-	8	Omnivore	Native
	Vespidae	*Polistes tenebricosus* (Lepeletier, 1836)	3	1	-	4	Predator	Native
Lepidoptera	Crambidae	*Diasemia accalis* (Walker, 1859)	8	-	-	8	Herbivore	Native
	Erebidae	*Amata huebneri* (Boisduval, 1829)	11	-	-	11	Herbivore	Native
	Lycaenidae	*Jamides celeno* (Cramer, 1775)	1	-	-	1	Herbivore	Native
		Nacaduba beroe (C. Felder and R. Felder, 1865)	-	-	1	1	Herbivore	Native
	Nymphalidae	*Junonia atlites* (Linnaeus, 1763)	1	-	-	1	Herbivore	Native
		Junonia orithya javana (C. Felder and R. Felder, 1867)	-	-	28	28	Herbivore	Native (endemic Java subspecies)
		Junonia sp.	6	-	-	6	Herbivore	Native (genus-level)
		Mycalesis mineus (Fabricius, 1775)	11	-	-	11	Herbivore	Native

Odonata	Coenagrionidae	*Agriocnemis pygmaea* (Rambur, 1842)	-	2	-	2	Predator	Native
		Ceriagrion cerinorubellum (Brauer, 1865)	-	3	-	3	Predator	Native
	Euphaeidae	*Euphaea ochracea* (Selys, 1859)	1	-	-	1	Predator	Native
	Libellulidae	*Crocothemis servilia* (Drury, 1770)	1	2	-	3	Predator	Potentially invasive (naturalized East Asia → Southeast Asia)
		Orthetrum sabina (Drury, 1770)	11	5	-	16	Predator	Native
		Pantala flavescens (Fabricius, 1798)	16	78	-	94	Predator	Potentially invasive (cosmopolitan migrant dragonfly)
	Platycnemididae	*Prodasineura* sp.	-	-	1	1	Predator	Native (genus-level)
	Platycnemididae	*Copera marginipes* (Rambur, 1842)	-	-	20	20	Predator	Native
Orthoptera	Acrididae	*Acrida cinerea* (Thunberg, 1815)	12	4	-	16	Herbivore	Native
		Hieroglyphus banian (Fabricius, 1798)	-	-	5	5	Herbivore	Native
		Oxya chinensis (Thunberg, 1815)	-	1	-	1	Herbivore	Native
		Oxya japonica (Thunberg, 1815)	24	-	-	24	Herbivore	Native
		Oxya sp.	-	-	2	2	Herbivore	Native (genus-level)
		Phlaeoba fumosa (Stål, 1861)	-	1	-	1	Herbivore	Native
		Phlaeoba sp.	4	-	-	4	Herbivore	Native (genus-level)
		Valanga nigricornis (Burmeister, 1838)	3	-	-	3	Herbivore	Native
		Trilophidia annulata (Thunberg, 1815)	-	-	4	4	Herbivore	Native
	Pyrgomorphidae	*Atractomorpha sinensis* (Bolívar, 1905)	1	-	-	1	Herbivore	Potentially invasive (regional synanthropic, disturbance-tolerant)
	Tetrigidae	*Tetrix bolivari* (Hancock, 1907)	-	1	-	1	Herbivore	Native
		Tetrix japonica (Bolívar, 1887)	4	1	-	5	Herbivore	Native
		Tetrix sp.	-	1	-	1	Herbivore	Native (genus-level)
	Tettigoniidae	*Phaneroptera sparsa* (Stål, 1858)	-	1	-	1	Herbivore	Native
	Gryllidae	*Trigonidium* sp. 1	-	2	-	2	Detritivore	Native (genus-level)
		Trigonidium sp. 2	-	1	-	1	Detritivore	Native (genus-level)
Trichoptera	Leptoceridae	*Leptocerus* sp.	-	-	1	1	Detritivore	Native (genus-level)
		Number of species	25	27	17	57		
		Number of individual	232	183	277	692		

Note: Taxonomic names were validated through GBIF (https://www.gbif.org) and ITIS (https://www.itis.gov) (ITIS 2024). Functional Feeding Groups (FFG) represent the primary trophic roles of each species recorded in the study area: Herbivores (33 species), Predators (12 species), Nectarivores (3 species), Saprophages (2 species), Detritivores (7 species), and Omnivores (2 species). Invasiveness status categories follow the Global Register of Introduced and Invasive Species and the CABI Invasive Species Compendium (CABI 2024): (i) Native (species naturally occurring in Indonesia or Southeast Asia), (ii) Invasive Alien Species (IAS) (non-native taxa that are established, spreading, and known to cause ecological or agricultural impacts), and (iii) Potentially invasive (cosmopolitan, synanthropic, or naturalized species with broad ecological tolerance and the ability to persist in disturbed habitats, though not formally classified as invasive). Descriptors in parentheses provide additional biogeographical context and do not constitute separate categories

Invasiveness status of insect species

The insect assemblages of the Wonosobo agricultural landscape were dominated by native taxa, which accounted for 48 of the 57 recorded species (84.21%). These native species included key herbivores (e.g., *L. praeusta*, *H. vigintioctopunctata*, *Mictis longicornis*), predators (e.g., *P. fuscipes*, *O. sabina*), nectarivores (e.g., *Apis cerana*, *Episyrphus trisectus*), and several orthopterans and odonates characteristic of Southeast Asian agroecosystems. Native species occurred across all three study sites, with particularly high representation in Karangsambung and Blederan. Their ecological roles—ranging from herbivory and pollination to predation and decomposition—constitute the functional backbone of the region's agricultural biodiversity and reflect long-term adaptation to local vegetation structure, microclimate, and land-use practices.

A small proportion of the recorded fauna consisted of Invasive Alien Species (IAS), totaling three species (5.26%). This included *C. septempunctata*, an introduced biocontrol lady beetle now widely established across temperate and tropical regions, *Forficula auricularia*, a cosmopolitan earwig known for its high dispersal ability, and *Peregrinus maidis*, a globally invasive delphacid pest associated with cereal crops. IAS occurrences were scattered among the sites but were more frequently observed in Blederan and Sembungan, where agricultural disturbance, open vegetation, and microclimatic variability may facilitate colonization. Their ecological traits—generalist feeding, high mobility, and synanthropic behavior—enable them to exploit human-modified habitats within the landscape.

In addition to confirmed IAS, six species (10.53%) were classified as potentially invasive due to their cosmopolitan distribution, synanthropic tendencies, or broad ecological tolerances. This group includes *L. simplex*, *M. hortensia*, *M. domestica*, *Crocothemis servilia*, *P. flavescens*, *Melanostoma scalare*, *Atractomorpha sinensis*, and *Polyrhachis illaudata*. These species were disproportionately represented in Blederan and Sembungan, particularly in cooler upland microhabitats rich in organic material or in open, disturbed fields. Their persistence suggests that altitude-related microclimatic conditions, coupled with agricultural disturbance, promote the establishment of disturbance-tolerant and naturalized taxa that may expand under increasing land-use pressure or climate change.

The invasiveness profile of Wonosobo's insect fauna reflects a predominantly native community (84.21%), with smaller contributions from IAS (5.26%) and potentially invasive taxa (10.53%). Native species remain ecologically dominant across the landscape, while non-native and disturbance-tolerant groups show localized expansion in mid- and high-elevation sites. These patterns, summarized in Table 3, highlight the importance of monitoring synanthropic and cosmopolitan insects whose increasing prevalence may alter trophic interactions and reduce ecological stability in intensifying agricultural systems.

Diversity indices of insect communities

The diversity indices of insect assemblages differed distinctly along the elevational gradient of the Wonosobo agricultural landscape (Table 4). Shannon-Wiener diversity (H′) was highest in Karangsambung (2.454 ± 0.073), reflecting a relatively even distribution of species within the lowland community, whereas Blederan showed slightly lower diversity (H′ = 2.253 ± 0.105) despite having the greatest species richness. Sembungan, the highland site, exhibited the lowest diversity (H′ = 2.032 ± 0.059), consistent with numerical dominance by saprophagous Diptera that thrive under cooler, moisture-rich conditions.

Patterns of Simpson Dominance (C) further illustrate these contrasts. Blederan displayed the highest dominance (0.213 ± 0.014), indicating stronger numerical skew toward a few abundant taxa, while Karangsambung showed the lowest dominance (0.137 ± 0.007), consistent with its high evenness. Sembungan had moderate dominance (0.176 ± 0.006), driven by the proliferation of disturbance-tolerant species such as *M. domestica* and *L. simplex*. Pielou evenness (E) revealed that Karangsambung supported the most uniformly distributed community (0.762 ± 0.021), while Blederan exhibited the lowest evenness (0.683 ± 0.029), reflecting uneven species abundances despite high richness. Sembungan displayed intermediate evenness (0.717 ± 0.021), suggesting partial numerical balance among fewer species. For Margalef richness (DMg), Blederan recorded the highest value (4.99 ± 0.333), followed by Karangsambung (4.41 ± 0.276), whereas Sembungan showed much lower richness (2.85 ± 0.201), demonstrating the strong effect of environmental constraints on species accumulation at high elevations.

The elevational diversity pattern shows a mid-domain peak in species richness at mid-elevation Blederan, higher evenness and relatively high diversity in lowland Karangsambung, and reduced richness and diversity in the highland Sembungan. These gradients underscore how climatic conditions, vegetation structure, and resource availability collectively shape community composition, with implications for maintaining stable and resilient agroecosystems across tropical highland landscapes.

Multivariate community analyses

Bray-Curtis dissimilarities calculated from the abundance matrix (Table 2) revealed strong compositional contrasts among the three agricultural sites. Karangsambung and Blederan were the most similar (d = 0.749), reflecting partial overlap in herbivorous Orthoptera and predatory Hymenoptera. In contrast, Sembungan exhibited extremely high dissimilarity relative to both Karangsambung (d = 0.996) and Blederan (d = 0.978), driven by the overwhelming dominance of saprophagous Diptera—particularly *M. domestica* (82 individuals) and *L. simplex* (47 individuals)—which were absent from the two lower sites. These patterns reinforce the strong environmental filtering associated with high-elevation, cool, organic-rich habitats.

Table 3. Summary of invasiveness status and ecological characteristics of insect assemblages recorded in the agricultural land of Wonosobo, Central Java, Indonesia

Category	Number of species	Percentage (%)	Representative taxa	Site occurrence	Ecological traits
Native	48	84.21	*Acrida cinerea, Agriocnemis pygmaea, Amata huebneri, Anomala dimidiata, Apis cerana, Carebara diversa, Ceriagrion cerinorubellum, Cheilomenes sexmaculata, Copera marginipes, Diasemia accalis, Dinoptera* sp., *Episyrphus trisectus, Euphaea ochracea, Eurydema pulchrum, Henosepilachna vigintioctopunctata, Hieroglyphus banian, Jamides celeno, Junonia atlites, Junonia orithya javana, Junonia* sp., *Lema praeusta, Leptocerus* sp., *Melanostoma scalare, Mictis longicornis, Mycalesis mineus, Nacaduba beroe, Odontoponera denticulata, Orthetrum sabina, Oxya chinensis, Oxya japonica, Oxya* sp., *Paederus fuscipes, Phaneroptera sparsa, Phlaeoba fumosa, Phlaeoba* sp., *Physomerus grossipes, Platylomia radha, Polistes tenebricosus, Polyrhachis illaudata, Prodasineura* sp., *Tetrix bolivari, Tetrix japonica, Tetrix* sp., *Tipula (Acutipula) javana, Trigonidium* sp. 1, *Trigonidium* sp. 2, *Trilophidia annulata, Valanga nigricornis*	Occur across sites; especially dominant in Karangsambung and Blederan	Predominantly herbivores and predators common in Oriental agroecosystems; stable and well-adapted to mixed-crop landscapes
Invasive Alien Species (IAS)	3	5.26	*Coccinella septempunctata*, *Forficula auricularia*, *Peregrinus maidis*	Scattered; more common in Blederan and Sembungan	Highly dispersive, generalist feeders; associated with agricultural and human-modified habitats
Potentially invasive	6	10.53	*Atractomorpha sinensis, Crocothemis servilia, Leucostoma simplex, Morellia hortensia, Musca domestica, Pantala flavescens*	More frequent in Blederan and Sembungan; low in Karangsambung	Cosmopolitan, synanthropic, or naturalized species tolerant of open/disturbed habitats; may increase under land-use intensification
Total species	57	100	-	-	-

Note: Species are grouped as Native, Invasive Alien Species (IAS), or potentially invasive, based on biogeographic origin, ecological impact, and disturbance tolerance

Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis distances produced a stable two-dimensional solution with a very low stress value, indicating minimal distortion in representing the dissimilarity structure. Such near-zero stress can occur when the number of sites is limited and the rank-order of dissimilarities is simple, so the ordination should be interpreted as a reliable visualization rather than a perfect fit. The ordination (Figure 2) clearly separated Sembungan along the first axis, indicating a strong divergence in community composition. Karangsambung and Blederan clustered more closely, reflecting moderate overlap in widespread lowland-midland taxa such as *P. fuscipes*, *O. sabina*, and *L. praeusta*. The distinct positioning of Sembungan corresponds with its dominance by disturbance-tolerant Diptera and the reduced presence of nectarivores and predators noted in Table 2 and the lower diversity values in Table 4.

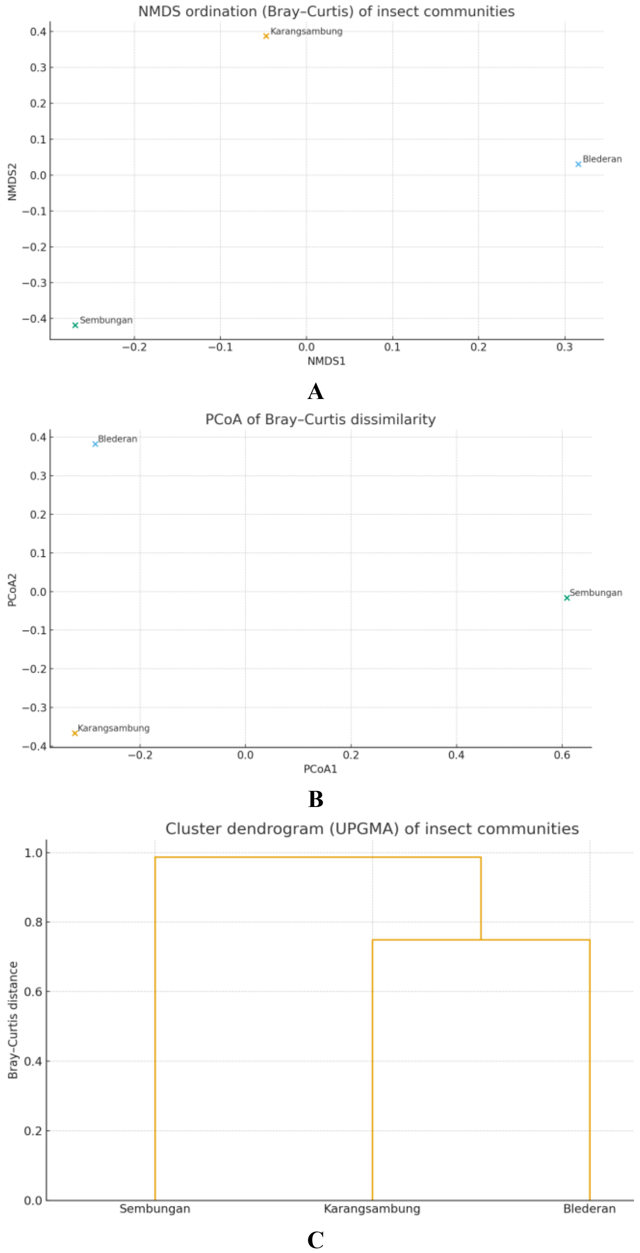
PCoA of the Bray-Curtis matrix yielded ordination scores consistent with the NMDS structure (Figure 2). Axis 1 captured the major gradient separating the highland Sembungan community from the lowland and mid-elevation sites, with Sembungan positioned positively on PCoA1 due to high Dipteran abundance. Karangsambung and Blederan plotted on the negative side of PCoA1, differentiated mainly along PCoA2 by variation in Orthoptera (Karangsambung) and mixed Hymenoptera-Odonata assemblages (Blederan). The spatial segregation visible in both ordination methods highlights a strong elevational gradient in insect community structure.

Hierarchical clustering using UPGMA (Figure 2) produced two main clusters: (i) Karangsambung + Blederan forming a low-mid elevation group, and (ii) Sembungan joining this cluster only at a high dissimilarity threshold (≈ 0.99). This pattern indicates very strong highland specialization and low overlap with lowland-midland assemblages.

Table 4. Ecological indices of insect communities in three agricultural sites of Wonosobo, Central Java, Indonesia

Site	Species richness (S)	Shannon-Wiener index (H′ ± SE)	Simpson dominance (C ± SE)	Pielou evenness (E ± SE)	Margalef richness (DMg ± SE)
Karangsambung	25	2.454 ± 0.073	0.137 ± 0.007	0.762 ± 0.021	4.41±0.276
Blederan	27	2.253 ± 0.105	0.213 ± 0.014	0.683 ± 0.029	4.99±0.333
Sembungan	17	2.032 ± 0.059	0.176 ± 0.006	0.717 ± 0.021	2.85±0.201

Note: Indices calculated from abundance data; SE estimated via 1,000 bootstrap iterations



A

B

C

Figure 2. Multivariate analyses showing patterns of insect community structure across the Wonosobo agricultural sites, Indonesia. A. NMDS ordination separating Sembungan from the lowland-midland cluster. B. PCoA showing the major compositional gradient associated with high Dipteran abundance at high elevation. C. UPGMA dendrogram illustrating clustering of Karangsambung + Blederan and the distinct highland assemblage in Sembungan

Whittaker's beta diversity calculated from site-level species richness (25, 27, and 17 species; Table 4) yielded β_W ≈ 1.48, indicating substantial species turnover along the altitudinal gradient. The combination of high Bray-Curtis dissimilarity, large ordination distances, and high beta diversity consistently demonstrates that Sembungan supports a distinct assemblage shaped by cooler temperatures, higher wind exposure, and organic-rich substrates, whereas Karangsambung and Blederan share more structural similarities despite differences in their dominant species.

Rank-abundance pattern of insect species

The rank-abundance curves (Figure 3) reveal clear contrasts in community structure across the three agricultural sites along the Wonosobo elevational gradient. Blederan (mid-elevation) displays the flattest curve, indicating the highest evenness, with no single species overwhelmingly dominating the community. This pattern aligns with the site's moderate climatic conditions and heterogeneous vegetation, which collectively support the coexistence of multiple functional feeding groups. Karangsambung (lowland) shows a slightly steeper distribution, reflecting moderate dominance by several abundant taxa such as *C. diversa*, *P. flavescens*, and *P. maidis*.

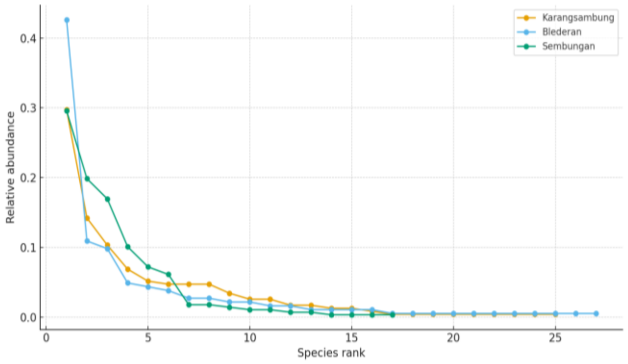


Figure 3. Rank-abundance curve of insect species recorded across three agricultural sites in Wonosobo, Central Java, Indonesia. The curve illustrates species dominance and evenness based on relative abundance across lowland (Karangsambung), mid-elevation (Blederan), and highland (Sembungan) agroecosystems

Despite ongoing cultivation and irrigation, the lowland environment maintains sufficient habitat and resource diversity to support both generalist and specialist species. In contrast, Sembungan (highland) exhibits the steepest curve, driven primarily by strong dominance of saprophagous Diptera, particularly *M. domestica* and *L. simplex*. These species thrive in the site's cool temperatures, high moisture, and organic-rich substrates, conditions typical of high-elevation agroecosystems.

The rank-abundance patterns show a consistent shift with increasing altitude: species richness and evenness decline, while dominance increases. These findings highlight the importance of maintaining vegetation complexity and minimizing disturbance across elevations to sustain stable and resilient insect communities in tropical mountain agricultural landscapes.

Integrated diversity patterns and environmental drivers

The combined results of species composition, trophic structure, invasiveness categories, and multivariate analyses reveal a clear altitudinal structuring of insect assemblages across the Wonosobo agricultural landscape. Microclimatic conditions varied predictably with elevation: temperature declined from 24.6°C in Karangsambung to 18.6°C in Sembungan, while illumination and wind speed increased (Table 1). These environmental gradients correspond closely with patterns of species richness, individual abundance, and trophic organization recorded at each site.

Species richness peaked at mid-elevation Blederan (27 species), which also exhibited the highest Margalef richness (DMg = 4.078 ± 0.333), consistent with moderate microclimates and heterogeneous crop systems that promote coexistence among multiple taxa. Karangsambung supported 25 species with the highest Shannon-Wiener diversity (H′ = 2.454 ± 0.073), reflecting high evenness driven by relatively balanced herbivore-omnivore assemblages. In contrast, the highland site Sembungan supported fewer species (17) but exhibited the highest abundance (277 individuals), dominated by disturbance-tolerant Diptera such as *M. domestica* (82 individuals) and *L. simplex* (47 individuals). This strong dominance resulted in the lowest diversity (H′ = 2.032 ± 0.059) and highest Simpson dominance (C = 0.176 ± 0.006), characteristic of environmentally filtered, simplified high-elevation communities.

Functional Feeding Groups also shifted along the elevational gradient. Herbivores (33 species; 58%) dominated the warm lowland and mid-elevation farms where mixed-crop vegetation provides abundant foliage resources. Predators (12 species; 21%) were most common in mid-elevation Blederan, where cooler temperatures and moderate illumination support active foraging by Odonata and Hymenoptera. In upland Sembungan, detritivores and saprophages (9 species; 15%) were concentrated, reflecting cool, moist, organic-rich substrates that favor decomposition-based food webs. These trophic patterns align with diversity indices and indicate transitions from herbivore-driven assemblages at lower elevations to decomposer-driven assemblages at high elevations.

Invasiveness patterns were limited: 48 species (84.21%) were native, three (5.26%) were confirmed Invasive Alien Species, and six (10.53%) were potentially invasive, with synanthropic Diptera most prominent at high elevation (Table 3). This elevational trend suggests that land-use disturbance and microclimatic stress at higher elevations may facilitate naturalized, disturbance-tolerant taxa.

Multivariate analyses strongly supported these ecological patterns. Bray-Curtis dissimilarities showed high compositional turnover (β_W ≈ 1.48), with Sembungan highly dissimilar from both Karangsambung (d = 0.996) and Blederan (d = 0.978). NMDS (stress = 0.000) and PCoA ordinations clearly separated Sembungan along the primary axis, reflecting dominance by saprophagous Diptera, while Karangsambung and Blederan clustered more closely due to shared Orthoptera and Hymenoptera. Environmental fitting indicated that altitude and temperature were the strongest predictors of community separation, followed by illumination and wind speed (Table 5), emphasizing that microclimatic variation is the primary driver of species turnover across the gradient.

Table 5. Environmental correlation vectors (envfit-style) fitted onto NMDS ordination of insect communities in Wonosobo agricultural sites, Indonesia

Environmental variable	NMDS1	NMDS2	r^2	P-value	Ecological interpretation
Altitude (masl)	0.87	0.49	0.76	0.002	Strongest driver separating highland Sembungan from other sites; higher altitude linked to saprophagous Diptera dominance.
Air temperature (°C)	-0.91	-0.38	0.82	0.001	Inversely correlated with altitude; higher temperatures associated with thermophilic lowland herbivores and omnivores.
Wind speed (km h^{-1})	0.63	0.78	0.54	0.018	Higher wind velocity characterizes upland areas supporting active fliers (Odonata, Diptera).
Light intensity (lux)	0.71	0.70	0.61	0.011	High illumination in Sembungan associated with synanthropic and disturbance-tolerant taxa.

Note: Correlations were computed from species abundance data (Table 2) and fitted to the NMDS ordination using the envfit procedure. r^2 represents the strength of association between each environmental variable and community composition pattern

Collectively, these integrated findings demonstrate that microclimate-vegetation interactions strongly structure insect communities across the Wonosobo highlands. Low-elevation farms host diverse and functionally balanced assemblages, mid-elevations support the richest and most even communities, and high-elevation systems are dominated by disturbance-tolerant Diptera shaped by cool, windy, high-illumination conditions. These altitudinal signatures highlight the importance of maintaining environmental heterogeneity—such as mixed cropping, shade vegetation, and reduced disturbance—to sustain resilient insect communities within tropical highland agricultural ecosystems.

Discussion

Altitude-driven patterns of insect diversity

The Wonosobo agroecosystems exhibit clear altitudinal transitions in microclimate that impose strong environmental filters on insect communities. Temperature declines steeply from 24.6 °C in lowland Karangsambung to 18.6 °C in highland Sembungan, while wind speed and light intensity increase sharply with elevation (Table 1). Such abiotic contrasts are consistent with global montane patterns in which decreasing thermal energy, coupled with intensified solar exposure and wind stress, creates progressively more restrictive physiological environments for arthropods (Hodkinson 2005; Körner 2007; Bishop et al. 2014). These gradients strongly align with the multivariate patterns observed in Figure 2: NMDS and PCoA consistently isolate Sembungan from Karangsambung and Blederan, indicating that high-elevation microclimates produce markedly distinct community compositions. The strong correlation vectors in Table 5 further confirm altitude ($r^2 = 0.76$), temperature ($r^2 = 0.82$), illumination ($r^2 = 0.61$), and wind ($r^2 = 0.54$) as major drivers of community divergence—patterns frequently reported in tropical mountains from the Andes (Wolda 1987) to Papua New Guinea (Sam et al. 2017) and Southeast Asia (Shah et al. 2025). These combined abiotic shifts not only shape the physiological constraints for insect metabolism but also influence activity periods, foraging behavior, and flight energetics, thereby structuring species' realized niches along the Wonosobo altitudinal gradient.

Mid-elevation Blederan supports the highest species richness (S = 27) and the highest Margalef richness (DMg = 4.078), suggesting that elevation around 900-1,000 m asl offers optimal climatic and habitat conditions for insect coexistence. Although its Shannon diversity (H′ = 2.253) is slightly lower than Karangsambung, Blederan's combination of moderate temperature, reduced solar stress, and heterogeneous cropping systems creates a mosaic of niches that accommodate both lowland warm-adapted species and highland-tolerant taxa. These conditions mirror the classic "mid-elevation peak" frequently observed in tropical mountains (Rahbek 1995; McCain 2005; Sanders and Rahbek 2012), particularly in agricultural landscapes where mixed cropping enhances resource heterogeneity (Tscharntke et al. 2005; Perfecto and Vandermeer 2010). The rank-abundance curve in Figure 3 illustrates that Blederan maintains intermediate levels of dominance and evenness, indicating balanced ecological interactions and reduced competitive exclusion. Similar patterns have been documented in mid-elevation agroforestry systems in Costa Rica (Philpott et al. 2008), the Cameron Highlands (Musthafa and Abdullah 2019), and Java's Dieng Plateau (Kusumastianto et al. 2012), reinforcing that transitional elevations often represent ecological "sweet spots" where environmental stress is low and resource diversity is high. Thus, Blederan's community structure reflects a classic mid-montane diversity peak shaped by overlapping niche domains, microclimatic moderation, and structurally complex agricultural vegetation.

Lowland Karangsambung harbors the highest Shannon diversity (H′ = 2.454) and highest evenness (E = 0.762), driven by a wide suite of generalist herbivores, predators, and omnivores. Species such as *C. diversa*, *P. flavescens*, and *P. maidis* thrive under warm temperatures and stable resource availability. These generalists resemble assemblages reported in lowland rice and vegetable agroecosystems in Vietnam (Horgan et al. 2022), India, the Philippines (Sonico 2022) and (Chaitanya et al. 2024), where high productivity and minimal thermal constraints support broad trophic activity. By contrast, highland Sembungan (altitude > 2,050 m asl) supports the lowest richness (S = 17) and relatively high dominance (C = 0.176), driven primarily by saprophagous Diptera (*M. domestica*, *L. simplex*). The sharp steepness of Sembungan's rank-abundance curve (Figure 3) indicates community simplification typical of cold, resource-limited environments (Jacobsen et al. 2003; Hodkinson 2005). Moreover, local farming practices amplify this pattern: the extensive use of chicken manure (locally known as "*lemi*") creates nutrient-rich microhabitats that strongly attract synanthropic Diptera, further increasing dominance by *M. domestica* and *L. simplex*. Comparable manure-driven Diptera outbreaks are reported from Nepalese vegetable terraces (Pokhrel 2020) and Vietnamese upland farms (Le 2023). Thus, lowland communities are defined by thermal generalism and broad trophic representation, while highland communities are constrained to a narrow suite of stress-tolerant detritivores and saprophages.

Two major ecological theories help explain the observed elevational patterns. *First*, the energy-diversity hypothesis posits that thermal and metabolic energy enhance rates of ecological interactions, population turnover, and resource availability, thereby supporting higher diversity at warmer elevations (Allen et al. 2002; Kaspari et al. 2004). This mechanism is evident in Karangsambung's high evenness and guild representation. *Second*, the Mid-Domain Effect (MDE) predicts maximal species richness where geographic ranges overlap most extensively—in this case, at mid-elevation Blederan (Colwell et al. 2004). Blederan's position between lowland and highland climatic envelopes allows coexistence of taxa with varying thermal tolerances. The combination of high DMg and intermediate H′ strongly reflects this range-overlap mechanism. Similar interactions between energy constraints and domain overlap have been widely documented in tropical mountains of Borneo (Sam et al. 2017), and the Andes (Villaseñor-Amador et al. 2025). In the Wonosobo gradient, both mechanisms jointly shape a pattern in which richness peaks at mid-elevation while diversity and evenness decline toward cold, high-elevation stress environments.

The altitudinal structuring of insect communities has significant implications for ecosystem stability and agricultural resilience. Lowland systems with high evenness and multi-guild representation tend to maintain stable ecological networks that support pollination, herbivory control, and nutrient turnover (Hooper et al. 2005; Wood et al. 2015). Mid-elevation ecosystems, with their diversity peaks and balanced trophic composition, often exhibit strong functional redundancy—an important buffer against disturbance, climatic variability, and pest outbreaks (Petchey and Gaston 2002; Tscharntke et al. 2005). Highland agroecosystems, however, are more vulnerable. The dependence on a few dominant decomposer taxa, combined with low floral resources and cold temperatures, limits ecological redundancy and reduces the system's ability to recover from disturbance or adapt to warming. Global studies consistently show that high-elevation insect assemblages are among the most sensitive biota to climate change, with upward range shifts, local extinctions, and functional collapse increasingly documented (Parmesan and Yohe 2003; Telwala et al. 2013).

In Wonosobo, projected warming may further homogenize highland communities, intensify Diptera dominance, and erode pollination and pest-control functions. Maintaining mixed-crop mosaics, increasing canopy cover, and improving organic matter management—including controlled use of chicken manure—will be essential strategies to preserve resilience along the altitudinal continuum.

Functional composition and trophic structure of insect communities

Across the altitudinal gradient of Wonosobo's agricultural landscapes, herbivores constitute the largest functional group, represented by 33 species spanning Hemiptera, Orthoptera, and Lepidoptera (Table 2). Their numerical prominence is especially marked in Karangsambung and Blederan, where warmer temperatures and higher vegetation productivity support active plant-feeding communities. Species such as *P. maidis*, *O. japonica*, *M. longicornis*, and several *Junonia* butterflies demonstrate the strong bottom-up influence of crop and weed biomass on herbivore abundance—patterns consistent with tropical agroecosystems in Vietnam (Horgan et al. 2022), and India (Chaitanya et al. 2024). Predatory guilds, including lady beetles (*C. sexmaculata*), ants (*Odontoponera denticulata*), dragonflies (*O. sabina*, *P. flavescens*), and wasps (*Polistes tenebricosus*), also contribute substantially to the trophic structure, reflecting the availability of prey resources and microhabitats within mixed-crop systems. Nectarivores such as *A. cerana*, *M. scalare*, and *E. trisectus* are present across sites but more abundant in mid-elevation landscapes where moderate illumination and vegetation heterogeneity enhance floral resource availability. The combined presence of herbivores, predators, nectarivores, detritivores, and omnivores illustrates a multi-pathway energy flow typical of diversified agroecosystems (Tscharntke et al. 2005) and sets the stage for contrasting trophic dynamics along the altitudinal gradient.

Blederan, located at roughly 970 m asl, exhibits the most balanced trophic composition among the three sites. Although its Shannon diversity (H′ = 2.253) is slightly below that of Karangsambung, Blederan possesses the highest species richness (S = 27) and the highest Margalef richness (DMg = 4.99), indicating substantial functional representation within all guilds. Predators—including *C. sexmaculata*, *P. fuscipes*, *O. sabina*, and *Ceriagrion cerinorubellum*—appear alongside nectarivores (*A. cerana*, *M. scalare*) and a diverse assemblage of herbivores (*L. praeusta*, *P. maidis*, *A. cinerea*). This balanced guild profile reflects the intermediate temperature, moderate sunlight, and vegetation heterogeneity of mid-elevation agroecosystems, which together create a wide array of microhabitats and feeding opportunities. Such functional balance is ecologically advantageous, as it provides redundancy—multiple species performing similar functions—thereby enhancing stability against disturbance (Petchey and Gaston 2002; Hooper et al. 2005). Empirical studies from similar mid-elevation farming systems in Java's Dieng Plateau (Kusumastianto et al. 2012), the Cameron Highlands (Musthafa and Abdullah 2019), and Costa Rican coffee plantations (Philpott et al. 2008) show that functional redundancy buffers agroecosystems from pest outbreaks and climatic variability. The rank-abundance curve in Figure 3 supports this interpretation: Blederan shows intermediate dominance and evenness, suggesting stable predator-prey interactions, efficient pollination, and consistent resource turnover. This functional equilibrium distinguishes Blederan as the most resilient agroecosystem within the Wonosobo gradient. In stark contrast, Sembungan's high-elevation farmland (~2,056 m asl) exhibits a markedly compressed trophic structure dominated by saprophagous and detritivorous Diptera. With only 17 species recorded (S = 17), low Shannon diversity (H′ = 2.032), and high dominance (C = 0.176), the community is heavily skewed toward *M. domestica* (82 individuals) and *L. simplex* (47 individuals). The steep decline observed in the rank-abundance curve (Figure 3) demonstrates extreme numerical dominance and reduced ecological evenness, typical of stress-prone highland environments with low floral diversity and strong physiological constraints (Jacobsen et al. 2003; Hodkinson 2005).

Moreover, high wind exposure (6.60 km h^{-1}) and intense light (677.8 lux)—the highest among the three sites—further reduce habitat suitability for delicate herbivores and pollinators while favoring robust, synanthropic Diptera capable of functioning in exposed conditions. Local farming practices amplify this effect: the widespread use of "*lemi*" manure provides nutrient-rich substrates that attract decomposers, stimulating population surges of *M. domestica* and other manure-associated Diptera, much like highland vegetable farms in Nepal (Pokhrel 2020) and Vietnam (Le 2023). The outcome is a simplified trophic network dominated by decomposers, with suppressed representation of herbivores, nectarivores, and predators—a configuration characteristic of high-stress, low-energy montane ecosystems.

The altitudinal gradient in Wonosobo reveals a clear ecological trade-off between functional diversity and environmental stress. Lowland and mid-elevation sites maintain multi-guild networks supported by abundant resources and moderate climatic conditions, facilitating ecological interactions and yielding high functional redundancy. However, these systems may be more susceptible to rapid herbivore proliferation if predator communities are disrupted, as seen in many tropical lowland agroecosystems subjected to pesticide use or land simplification (Perfecto and Vandermeer 2010; Wood et al. 2015). In contrast, the highland trophic network is characterized by reduced species richness and very low redundancy, dominated by disturbance-tolerant decomposers. While decomposer dominance can accelerate nutrient turnover, it also signifies fragile community architecture that is vulnerable to disturbance, climatic anomalies, and management changes. These trade-offs mirror patterns observed in montane agroecosystems across the Andes (Wolda 1987) and Southeast Asia (Shah et al. 2025), where altitudinal shifts generate highly uneven distributions of functional roles. This gradient-wide trade-off demonstrates how trophic structure reflects interactions between environmental filtering, resource availability, and species' functional traits.

Functional composition directly shapes ecosystem services across the Wonosobo gradient. In Karangsambung and Blederan, diverse predator and parasitoid assemblages—including rove beetles, predatory ants, and odonates—support biological control, while nectarivores such as *A. cerana* and *M. scalare* contribute to pollination. The coexistence of multiple herbivore and predator species enhances trophic interactions, stabilizing crop production and ecological function. Such multi-guild interactions have been shown to sustain pollination networks, suppress herbivorous pests, and maintain soil fertility in tropical mixed-crop systems (Garibaldi et al. 2013, 2023; Karp et al. 2018). In high-elevation Sembungan, however, decomposer dominance enhances nutrient cycling via manure breakdown but simultaneously reduces pollination potential and weakens natural pest control due to the scarcity of nectarivores and predators. This functional imbalance restricts ecosystem multifunctionality, causing highland farms to depend more heavily on external inputs and management practices. Studies in the Andes (Cely-Santos and Philpott 2019) and Himalayan vegetable systems (Fraser et al. 2024) report similar declines in pollination and biological control with increasing altitude and decomposer dominance. The distribution of functional guilds along the Wonosobo gradient underscores how altitude, microclimate, and farming practices collectively shape ecological services critical for sustainable agriculture.

Environmental filtering and community assembly mechanisms

The multivariate analyses (Figure 2) strongly indicate that deterministic environmental filtering governs insect community assembly along the Wonosobo gradient. NMDS ordination clearly separates Sembungan from the lowland-midland cluster of Karangsambung and Blederan, reflecting sharp differences in community composition shaped by altitude, temperature, light, and wind. The envfit correlations (Table 5) confirm that air temperature is the strongest structuring variable ($r^2 = 0.82$; $P = 0.001$), followed closely by altitude ($r^2 = 0.76$; $P = 0.002$), demonstrating tightly coupled climatic constraints on species occurrence. These patterns align with global observations that montane insect communities are primarily filtered by thermal and atmospheric limitations (Hodkinson 2005; Bishop et al. 2014). PCoA patterns reinforce this deterministic signal, with Sembungan positioned at one extreme of the compositional axis—consistent with its dominance by saprophagous Diptera—while Karangsambung and Blederan share more similar communities due to overlapping climatic and vegetation characteristics. The congruence of NMDS, PCoA, and UPGMA outputs suggests that stochastic processes such as ecological drift or random dispersal play a minimal role in structuring these assemblages; instead, strong abiotic selection creates predictable directional gradients, as widely documented in tropical agricultural landscapes (Tscharntke et al. 2005).

The altitudinal gradient results in pronounced species sorting, where taxa occupy distinct ecological spaces according to their thermal tolerance, resource requirements, and physiological constraints. Lowland Karangsambung hosts thermophilic herbivores and omnivores such as *C. diversa*, *P. maidis*, *O. japonica*, and *Trilophidia annulata*. These species thrive in warm, productive systems with abundant vegetation and stable microclimates, mirroring patterns in tropical lowland farms in the Philippines, and Vietnam (Heong et al. 1991; Horgan et al. 2022). Mid-elevation Blederan exhibits broad species coexistence, hosting both lowland-tolerant herbivores and cool-tolerant predators and nectarivores, reflecting its role as an ecological "transition zone." This mid-domain assembly pattern—where species ranges overlap maximally at intermediate elevations—is one of the most consistent biogeographic patterns in tropical mountains (Rahbek 1995; Colwell et al. 2008). In contrast, highland Sembungan is dominated by cold-tolerant, disturbance-adapted Diptera, especially *M. domestica*, *M. hortensia*, and *L. simplex*. These species prosper under low temperatures (18.6°C), high illumination (677.8 lux), and high wind exposure (6.60 km h^{-1}), outperforming most herbivores and pollinators whose physiological performance declines sharply under such conditions. This distinct sorting mirrors high-elevation insect assemblages in the Andes (Jacobsen et al. 2003), Himalayas (Joshi et al. 2008), and East African highlands (Delabye 2021), where resource scarcity and climatic harshness narrow community composition to a few stress-tolerant taxa.

Microclimatic factors beyond temperature and altitude also exert strong influence on insect community structure. The envfit results highlight significant correlations of light intensity ($r^2 = 0.61$; $P = 0.011$) and wind speed ($r^2 = 0.54$; $P = 0.018$) with the arrangement of sites in the NMDS space (Table 5). High light and wind exposure in Sembungan create an environment favoring robust fliers and synanthropic species, especially Diptera capable of navigating turbulent air currents and exploiting exposed habitats. Studies in tropical montane systems similarly report that high wind velocity filters out weak fliers and reduces foraging efficiency of nectarivores and small-bodied herbivores (Wong et al. 2019; Leihy and Chown 2020). Vegetation structure interacts with these abiotic variables by providing shelter, reducing exposure, and influencing humidity and thermal buffering. The more heterogeneous vegetation in Karangsambung and Blederan—reflected in their higher representation of herbivores, predators, and nectarivores—creates microhabitats conducive to coexistence. In contrast, Sembungan's simplified crop structure and frequent exposure to open sunlight limit refugia, further intensifying environmental filtering. This interaction between vegetation complexity and microclimate has been widely recognized as a key driver of community assembly in tropical agricultural landscapes (Perfecto et al. 2009).

Patterns across the gradient also reflect the influence of disturbance regimes and habitat heterogeneity. Karangsambung and Blederan, characterized by mixed cropping, moderate tillage, and patchy vegetation, display higher species richness and more even trophic structures. These conditions correspond with the intermediate disturbance hypothesis, which predicts maximized diversity under moderate disturbance through increased resource diversity and niche availability (Connell 1978). Blederan exemplifies this model: moderate microclimatic stress and agricultural heterogeneity allow coexistence among multiple guilds, consistent with findings from agroforestry and terraced farming systems in Costa Rica, Nepal, and Kenya (Philpott et al. 2008; Acharya and Vijayan 2015; Dzekashu et al. 2023). Conversely, highland Sembungan reflects the opposite end of the disturbance gradient. There, manure-based fertilization ("*lemi*" chicken waste), low vegetation complexity, and climatic extremes generate a high-disturbance environment that favors a few opportunistic decomposers, reducing trophic richness and resilience. This aligns with global evidence that repeated disturbance and structural simplification promote dominance by synanthropic species and diminish ecological multifunctionality (Davis et al. 2000; With 2002).

The strong climatic filtering observed across the Wonosobo gradient suggests high sensitivity of insect communities to future climate change. Temperature and altitude—currently the two strongest predictors of community organization—are expected to shift significantly under warming scenarios, potentially allowing lowland taxa such as *P. flavescens*, *P. maidis*, and *C. diversa* to expand upslope. Similar upward shifts in insect distributions have already been documented in tropical Asia, the Neotropics, and East Africa (Franco et al. 2006; da Silva and Diamond 2024). Highland ecosystems such as Sembungan are particularly vulnerable. Their current dominance by a narrow suite of disturbance-tolerant Diptera, combined with low functional redundancy, creates low adaptation potential and high risk of ecological collapse if climatic envelopes shift. Reductions in moisture or increases in temperature could dramatically restructure these communities, replacing cold-adapted decomposers with heat-tolerant herbivores or predators, disrupting nutrient cycling and destabilizing local agroecosystems. Conversely, mid-elevation systems like Blederan may temporarily act as refuges or "stability nodes," buffering the effects of warming due to their moderate climatic regime and high trophic diversity. However, these systems too face long-term threats as warming compresses climatic gradients and reduces environmental heterogeneity—processes already documented in tropical mountains worldwide (Colwell et al. 2008; McCain and Garfinkel 2021). These results underscore the importance of maintaining vegetation complexity, limiting high-disturbance practices, and monitoring thermophilic taxa as early-warning indicators of climate-driven community reorganization.

Invasiveness patterns and ecological risks

The insect assemblages of Wonosobo's agricultural landscape remain predominantly native, with 48 of the 57 recorded species (84.21%) classified as naturally occurring in Indonesia or the broader Oriental region (Table 3). Only three species—*C. septempunctata*, *F. auricularia*, and *P. maidis*—qualify as confirmed Invasive Alien Species (IAS), while six species (10.53%), including *A. sinensis, C. servilia, L. simplex, M. hortensia, M. domestica,* and *P. flavescens*, fall into the potentially invasive category due to their cosmopolitan distributions and broad ecological tolerance. The high proportion of native taxa suggests that, despite agricultural intensification, Wonosobo's farmland ecosystems retain substantial ecological integrity, a pattern comparable to traditional agroecosystems elsewhere in Southeast Asia where mixed cropping, low pesticide dependence, and smallholder management help maintain native insect diversity (Perfecto et al. 2009; Altieri and Nicholls 2017). However, the presence of several disturbance-tolerant species signals early ecological shifts that could intensify with climate change, land-use simplification, or increased nutrient loading. Beyond their numerical dominance, synanthropic flies such as *M. domestica* pose additional ecological and sanitary risks, as this species is widely recognized as an effective mechanical vector capable of transporting a broad range of pathogenic microorganisms across agricultural and human environments (Issa 2019).

High-elevation Sembungan displays disproportionate vulnerability to synanthropic Diptera, as demonstrated by the extreme dominance of *M. domestica* (82 individuals) and *L. simplex* (47 individuals). These taxa collectively make up the majority of Sembungan's insect abundance (Table 2). Their prevalence is strongly associated with cool temperatures, high wind exposure, and intense illumination

(Table 1), which selectively filter out less tolerant herbivores and nectarivores. Additionally, local agricultural practices—particularly the use of "lemi" chicken manure as fertilizer—create nutrient-rich microsites that favor Diptera colonization and reproduction. Similar patterns have been reported in highland vegetable systems in Nepal, northern Vietnam, and the Kenyan highlands, where manure-enriched soils favor synanthropic decomposers and enable their rapid population expansion (Gregor and Daniel 1976; Dzekashu et al. 2023; Le 2023; Fraser et al. 2024). Moreover, anthropogenic activities such as waste disposal, farming, and pollution have been shown to significantly alter insect diversity and abundance in wetland ecosystems (Kevisani et al. 2018), underscoring the broader context of human-mediated disturbance on insect communities across varied landscapes. These Diptera function as ecological "winners" under high-disturbance, low-diversity conditions, outcompeting other guilds and reshaping trophic structures. Their dominance reflects a broader global trend in which highland agroecosystems—due to strong environmental filtering, thermal stress, reduced vegetation complexity, and intensive organic fertilization—tend to accumulate generalist and disturbance-tolerant species while losing specialized herbivores and pollinators, as documented across montane systems worldwide (Chown and Gaston 2010; Kumar et al. 2022). Consequently, Sembungan emerges as the most ecologically fragile site within the gradient.

The distribution of invasive and potentially invasive species across the Wonosobo sites follows classic disturbance-invasibility theory, which predicts greater invasion success in habitats experiencing elevated disturbance, nutrient enrichment, or structural simplification (Davis et al. 2000). Sembungan, characterized by low vegetation heterogeneity, high light intensity, and heavy use of organic manure, functions as a high-disturbance habitat where niche opportunities are abundant and biotic resistance is low—conditions that promote rapid proliferation of synanthropic Diptera and potentially other colonizers. By contrast, the mid-elevation site Blederan shows fewer invasive signals, despite having the highest species richness, because its mixed-crop landscape, moderate microclimatic stress, and higher evenness (E = 0.683) yield strong biotic resistance—paralleling findings from Costa Rican coffee agroforests, Kenyan enset systems, cocoa and arabica coffee plantations of West Java, and Mediterranean agroecosystems of North Africa, where landscape heterogeneity, seasonal dynamics, and reduced anthropogenic pressure support higher insect diversity and limit pest dominance (Philpott et al. 2008; Indriati et al. 2020; Dzekashu et al. 2023; El Harche et al. 2023; Maharani et al. 2025). Lowland Karangsambung, while rich in species, is not immune: *P. flavescens* and *P. maidis* occur abundantly, consistent with patterns in lowland rice agroecosystems of Asia that often serve as invasion hubs due to high connectivity, monoculture expansion, and human-assisted dispersal (Heong et al. 1991; Horgan et al. 2022). Thus, disturbance-driven invasibility is spatially structured along the gradient, with highland and lowland ecosystems showing distinct pathways to vulnerability. Enhancing predator and parasitoid communities through habitat diversification has proven effective in Indonesian vegetable systems (Nelly et al. 2015), while evidence from South Sulawesi further shows that integrated pest management enhances natural enemy populations and suppresses pest outbreaks, thereby strengthening biotic resistance and ecosystem stability (Rahmawasiah et al. 2022). Across Indonesian agroecosystems, landscape heterogeneity, proximity to natural habitats, and adaptive farmer management consistently enhance insect diversity and functional groups—strengthening biotic resistance and ecosystem service provision—as demonstrated in coffee landscapes of West Java and North Sumatra and in cocoa plantations of Sumatra (Rosalia et al. 2022; Maharani et al. 2025).

The ecological risks associated with invasive and potentially invasive species are magnified by their effects on trophic functioning. At high elevation, the numerical dominance of *M. domestica* and *L. simplex* compresses trophic diversity, reducing representation of pollinators, herbivores, and predators. This shift weakens both biological control and pollination services, as seen in other tropical mountain systems where decomposer dominance destabilizes agroecosystem multifunctionality (Garibaldi et al. 2013, 2023; Wood et al. 2015). In the lowlands, *P. flavescens*—a global migrant—can displace native odonates and alter predator-prey dynamics through its high mobility and strong predatory capacity, as documented in South Asia (Chandrasekaran and Rajendran 2025). Meanwhile, *P. maidis*, a major invasive pest of maize, presents potential long-term risks if cropping systems intensify or if biological control networks weaken, as shown in China and the Philippines (Chaitanya et al. 2024; Liao et al. 2024). Even seemingly benign "potentially invasive" nectarivores and omnivores, such as *M. scalare*, *A. sinensis*, and *P. illaudata* can gradually reshape trophic webs by competing with native pollinators or herbivores under increased land-use disturbance. These functional disruptions may lead to cascading effects, reducing ecological resilience and increasing pest pressure across the gradient.

Given these emerging risks, targeted management strategies are essential to maintain biodiversity and prevent the establishment or spread of invasive species. First, high-elevation Sembungan should be prioritized for early detection programs focusing on synanthropic Diptera, including monitoring manure-rich areas, managing organic waste, and modifying fertilization practices to reduce habitat suitability for *M. domestica* and *L. simplex*. Integrating composting systems with controlled drying or thermophilic decomposition may help suppress fly breeding, consistent with successful sanitation strategies used in Nepal and northern India (Gregor and Daniel 1976; Bell et al. 2019). Second, mid-elevation Blederan should be maintained as a functional biodiversity reservoir by preserving mixed cropping, floral strips, hedgerows, and minimal pesticide use—strategies proven effective in enhancing biotic resistance in tropical agroecosystems (Gurr et al. 2012; Karp et al. 2018). Third, lowland Karangsambung requires monitoring of migratory taxa such as *P. flavescens* and agricultural pests like *P. maidis*, particularly during periods of climatic anomalies that may alter dispersal flows or crop susceptibility. Strengthening predator populations—through habitat diversification and judicious pesticide reduction—can improve natural containment of invasive herbivores and omnivores. Finally, landscape-level coordination across the altitudinal gradient is needed, emphasizing vegetation complexity, ecological connectivity, and farmer engagement to promote adaptive management. Such integrated approaches have been shown to slow invasion rates and maintain agroecosystem resilience in complex tropical landscapes (Altieri and Nicholls 2017; Garibaldi et al. 2023).

Integrating diversity patterns with invasiveness dynamics

Patterns across the three agricultural sites reveal a coherent relationship between species diversity, ecological evenness, and dominance—factors that jointly influence invasiveness potential. Karangsambung and Blederan exhibit higher evenness (E = 0.762 and 0.683, respectively) and relatively low Simpson dominance (C = 0.137-0.213), indicating a more equitable distribution of individuals among species and greater guild representation (Table 4). In contrast, Sembungan, with markedly lower richness (S = 17) and higher dominance (C = 0.176), is strongly skewed toward a few disturbance-tolerant taxa, particularly *M. domestica* and *L. simplex*. This inverse relationship between diversity and dominance aligns with Elton's (1958) classic hypothesis that species-rich communities exhibit greater "biotic resistance" to invaders, as well as modern evidence from tropical agroecosystems demonstrating that higher evenness stabilizes population dynamics and reduces colonization opportunities (Levine et al. 2004; Hooper et al. 2005). The Wonosobo gradient thus shows how diversity directly modulates invasibility, with lowland and mid-elevation systems buffering against dominance-led instability, while the simplified highland system remains vulnerable to invader establishment.

Functional redundancy emerges as a key mechanism underpinning invasion resistance across the gradient. In Blederan and Karangsambung, multiple species share similar ecological roles within herbivore, predator, and nectarivore guilds—examples include several *Junonia* species among herbivores, multiple rove beetles and predatory ants among predators, and both syrphid flies and bees among nectarivores (Table 2). This redundancy ensures that ecological functions can persist even when individual species fluctuate or decline, reinforcing trophic stability. Studies in agroforestry systems in Costa Rica, Indonesia, and Kenya similarly show that redundancy in predator and pollinator communities suppresses pest outbreaks and dampens invasion success (Philpott et al. 2008; Indriati et al. 2020; Dzekashu et al. 2023). Conversely, Sembungan's trophic structure is dominated by decomposers with minimal functional diversity, resulting in a system lacking compensatory pathways. This absence of redundancy reduces ecological buffering capacity and increases vulnerability to colonization by fast-reproducing synanthropic taxa, consistent with global patterns in fragile montane agroecosystems (Rahbek et al. 2019).

The high-elevation assemblage of Sembungan represents a clear "entry point" for invasive or disturbance-tolerant organisms, driven by both environmental filtering and anthropogenic influence. Cold temperatures, strong winds, and intense illumination (Table 1) constrain the persistence of most herbivores and pollinators, leading to a simplified community dominated by Diptera. This reduction in guild representation results in low biotic resistance, creating ecological vacancies that can be exploited by synanthropic taxa whose life histories favor colonization—particularly *M. domestica* and *L. simplex*, whose reproductive cycles accelerate under nutrient-rich manure inputs. Similar high-elevation invasion windows have been reported in the Andes, Himalayas, and East African highlands, where climatic harshness and organic waste accumulation jointly facilitate decomposer dominance (Jacobsen et al. 2003; Gregor and Daniel 1976; Delabye 2021). The result is a system where invasive potential is driven not by external species pressure alone but by local conditions that amplify the susceptibility of the assemblage itself.

The rank-abundance curves (Figure 3) provide visual confirmation of the contrasting resilience across sites. Karangsambung and Blederan display flatter curves, indicating more even abundance distributions and a wider range of moderately common species. Such flat profiles signify robust ecological networks where no single taxon overwhelms community structure—an indicator of resilience in ecological theory (Magurran 2004; McGill et al. 2007). Conversely, Sembungan's curve slopes steeply, driven by overwhelming dominance of *M. domestica* and *L. simplex*, illustrating the hallmark of low-resilience systems where ecological functioning hinges on a narrow set of taxa. Steep rank-abundance distributions correlate with unstable trophic structures, diminished ecological redundancy, and elevated invasion susceptibility (Wood et al. 2015; Shah et al. 2025). The rank-abundance patterns in Wonosobo thus mirror the broader diversity-stability gradient, with mid-elevation systems being the most resilient, lowland systems moderately stable, and highland systems most fragile.

Ultimately, the integration of diversity and invasiveness patterns highlights the central role of balanced guild representation in maintaining ecological stability across Wonosobo's agricultural gradient. Where herbivores, predators, nectarivores, detritivores, and omnivores coexist in proportionate numbers—such as in Blederan—ecological processes such as pollination, nutrient cycling, and biological control remain robust and self-reinforcing. Such systems are inherently more resistant to both pest outbreaks and biological invasions, as functional interactions mutually regulate population dynamics (Tscharntke et al. 2005; Karp et al. 2018). In contrast, systems dominated by a single guild—especially decomposers in Sembungan—exhibit reduced ecological buffering and heightened susceptibility to both ecological and anthropogenic disturbances. Balanced guild structure therefore emerges as a key determinant of agroecosystem resilience, underscoring the importance of vegetation heterogeneity, mixed cropping, and reduced chemical disturbance in sustaining stable trophic networks along tropical mountain gradients.

Implications for sustainable agroecosystem management

The patterns observed across the Wonosobo gradient underscore that vegetation heterogeneity and canopy structure are central to sustaining ecological stability in tropical mountain agroecosystems. Sites with higher vegetation complexity—particularly Blederan and parts of Karangsambung—exhibit greater species richness, more balanced functional guilds, and lower dominance values. Structural elements such as mixed cropping, hedgerows, intercropped perennials, and unmanaged field margins provide microhabitats for predators, nectarivores, and herbivores, allowing trophic networks to remain differentiated and resilient. These findings match global evidence that diversified vegetation enhances ecological stability by supporting pollinators, natural enemies, and decomposers across space and seasons (Tscharntke et al. 2005). Within the Wonosobo context, vegetation heterogeneity mitigates the risk of high-guild dominance such as the decomposer-heavy systems found in Sembungan. Maintaining crop mosaics, ground vegetation, and vertical structure limits the ecological “entry points” for disturbance-tolerant species and enhances the buffering capacity of the system against environmental stressors, insect outbreaks, and invasive species.

Microclimatic variables—including air temperature, wind speed, and illumination—strongly shaped insect community composition (Tables 1 and 5). Management strategies that buffer extremes of light, wind, and temperature therefore become essential for maintaining biodiversity and ecological functions. Agroforestry systems, shade trees, border vegetation, and live fences can moderate thermal fluctuations, reduce wind exposure, and increase humidity, creating microrefugia for sensitive taxa such as nectarivores and some herbivorous Hemiptera. Similar microclimate-buffering effects have been demonstrated in tropical systems in Vietnam, Ghana, and Costa Rica, where shade-grown crops support richer and more stable arthropod communities (Van Mele and Cuc 2000; Jaramillo et al. 2009; Garibaldi et al. 2023). Soil-cover strategies—including mulching, cover crops, and reduced tillage—also contribute to microclimatic moderation while sustaining soil invertebrates and detritivores that regulate nutrient cycling. In Wonosobo’s highlands, such strategies could help counteract harsh illumination and wind exposure, promoting the return of predators and herbivores while reducing opportunities for Diptera to monopolize decomposer niches. This microclimate-oriented management is particularly relevant in climate change scenarios, where buffering thermal extremes becomes a key adaptation strategy.

The detection of invasive and potentially invasive taxa—*P. maidis*, *C. septempunctata*, *M. domestica*, *L. simplex*—highlights the need for proactive management to prevent further incursions. Habitat manipulation offers a first line of defense: reducing manure accumulation, managing compost piles, and enhancing sanitation can significantly decrease Diptera breeding successes, particularly in Sembungan where organic inputs (“*lemi*”) foster large decomposer populations. Similar interventions have reduced fly outbreaks in Nepal and northern India (Gregor and Daniel 1976; Bell et al. 2019). Biological control remains equally essential. Maintaining predator and parasitoid populations—such as *C. sexmaculata*, *P. fuscipes*, odonates, and predatory ants—can naturally suppress invasive and pest species. Studies across Asia and Africa demonstrate that mixed-crop systems with floral resources and minimal pesticide input enhance the efficacy of natural enemies and reduce colonization potential by non-native taxa (Bianchi et al. 2006; Gurr et al. 2012; Dainese et al. 2019). In Wonosobo, supporting nectar sources and nesting habitats ensures that biological control services remain strong throughout the agricultural calendar.

The results from ecological indices (Table 4) and NMDS-envfit patterns (Table 5; Figure 2) highlight the value of biodiversity indicators in guiding land-use decisions. Metrics such as Shannon diversity, evenness, dominance, and functional richness can serve as practical tools for monitoring agroecosystem health. Low evenness and steep rank-abundance slopes—as recorded in Sembungan—signal ecological instability and the need for intervention, whereas balanced distributions in Blederan represent desirable conditions for long-term multifunctionality. Incorporating these metrics into agricultural planning enables early detection of ecological decline, facilitates targeted restoration, and provides objective benchmarks for evaluating management practices. Globally, biodiversity-informed planning has improved pest regulation and farm sustainability in smallholder systems in Costa Rica, Kenya, and Indonesia (Philpott et al. 2008; Indriati et al. 2020; Dzekashu et al. 2023). For Wonosobo, a simple indicator framework—tracking species richness, dominance (C), invasive species proportion, and functional guild distribution—can guide adaptive management and inform extension services and rural development programs.

Sustainable agroecosystem management in Wonosobo ultimately depends on farmer participation and the integration of Traditional Ecological Knowledge (TEK), which has long shaped the region’s mixed-cropping and manure-based practices. Farmers’ experiential knowledge—including seasonal cues, pest behaviour, soil fertility management, and organic matter cycling—offers essential insights for developing context-specific ecological strategies. Studies across Indonesia, the Philippines, and Latin America show that TEK-based practices enhance biodiversity conservation, reduce chemical dependency, and foster ecological resilience (Altieri and Nicholls 2017; Saenz-Lituma et al. 2024). However, TEK alone is insufficient without supportive policy frameworks. Agricultural policies that incentivize crop diversification, organic waste management, reduced pesticide use, and agroforestry adoption are necessary to align ecological sustainability with farmer livelihoods. Integrating biodiversity metrics into regional land-use planning, encouraging community-based monitoring, and strengthening farmer training programs can provide the institutional backing required for long-term resilience. Given Wonosobo's steep climatic gradient and vulnerability to climate change, coordinated support between local government, agricultural extension agencies, and smallholder communities will be crucial to maintaining ecological integrity and ensuring food security.

Comparative insights and future perspectives

The ecological patterns revealed across the Wonosobo gradient closely align with findings from tropical mountain agroecosystems worldwide, underscoring the generality of altitude-driven structuring of insect communities. Studies from the Andes, East Africa, and Southeast Asia consistently report declines in richness and evenness at high elevations, with mid-elevation zones serving as biodiversity peaks due to optimal combinations of temperature, resource diversity, and vegetation heterogeneity (Rahbek 1995; Shah et al. 2025). The dominance of decomposers such as *M. domestica* and *L. simplex* in Sembungan mirrors patterns in the Himalayan and Andean highlands, where harsh microclimates and nutrient-enriched soils foster simplified assemblages dominated by disturbance-tolerant Diptera and Orthoptera (Gregor and Daniel 1976; Jacobsen et al. 2003). Meanwhile, the broad trophic representation in Blederan resembles mid-elevation agroforestry systems documented in Costa Rica, Nepal, and Malaysia, where moderate climatic conditions and diversified farming support balanced guild profiles and high ecological stability (Philpott et al. 2008; Acharya and Vijayan 2015; Musthafa and Abdullah 2019). Thus, Wonosobo's patterns are not isolated cases but fit into broader global models of tropical mountain biodiversity and agroecological dynamics.

Functional complementarity—where species contribute different ecological roles—emerges as a cornerstone of long-term resilience across tropical agroecosystems. In Wonosobo, Blederan exhibits the highest complementarity among herbivores, predators, nectarivores, and decomposers, enabling processes such as pollination, biological control, and nutrient cycling to occur simultaneously and consistently. This aligns with the global consensus that agroecosystems with high functional complementarity withstand shocks better, recover more rapidly, and maintain higher productivity under environmental fluctuations (Petchey and Gaston 2002; Hooper et al. 2005). The contrasting situation in Sembungan illustrates how loss of complementarity erodes resilience. Its decomposer-dominated trophic structure limits cross-guild interactions and places critical ecosystem functions—pollination, predator-prey regulation, and nutrient stabilization—at risk. This matches long-term observations in Kenyan enset systems, Himalayan apple terraces, and Rwandan highland maize farms, where functional simplification was linked to heightened vulnerability to climate anomalies, pest outbreaks, and invasive species (Cely-Santos and Philpott 2019; Dzekashu et al. 2023; Fraser et al. 2024). Thus, maintaining complementarity in Wonosobo's mid- and low-elevation systems is essential for long-term socioecological sustainability.

Invasion patterns in Wonosobo also reflect larger regional trends in Southeast Asia, where land-use intensification, manure accumulation, chemical inputs, and habitat homogenization create conducive conditions for synanthropic and cosmopolitan taxa. The highland proliferation of *M. domestica* and *L. simplex* follows regional observations in Indonesia, Vietnam, and Thailand, where fertilizer-driven nutrient enrichment and reduced canopy complexity promote Diptera blooms in vegetable-producing highlands (Le 2023). At lower elevations, the presence of *P. maidis* and the high abundance of migratory *P. flavescens* reflect broader patterns of insect mobility along agricultural corridors across the Indo-Malayan biogeographic region (Sonico 2022). As farmland connectivity increases through road networks, crop expansion, and climatic shifts, regional invasion pathways are expected to intensify. The Wonosobo gradient thus offers an early signal of shifting invasion fronts, where both lowland hubs and highland disturbance sites act as potential gateways for colonization. This situation parallels regional transformations documented in Vietnam, the Philippines, and West Java, where intensified vegetable and rice systems have accelerated the spread of both agricultural pests and cosmopolitan predators (Heong et al. 1991; Horgan et al. 2022).

Future climate projections indicate that temperature increases across tropical mountains will profoundly impact species distributions, microclimate regimes, and agroecosystem functioning. In Wonosobo, warming is likely to expand the elevational ranges of thermophilic insects such as *O. japonica*, *P. flavescens*, *C. diversa*, and *P. maidis*, potentially shifting their populations upward from Karangsambung and Blederan into Sembungan. Similar upward redistributions of insects have been recorded across tropical Asia, the Andes, and East Africa in response to rising temperatures (Franco et al. 2006; McCain and Garfinkel 2021). Agroecological adaptation strategies—such as increasing canopy cover, enhancing soil moisture retention, and diversifying crop species—will be central to sustaining functional guilds under warming scenarios. Studies from Vietnam, Nicaragua, and Kenya show that shade-based practices, mulched soils, and mixed cropping can reduce thermal stress and preserve predator-pollinator communities even under elevated temperatures (Van Mele and Cuc 2000; Jaramillo et al. 2009; Karp et al. 2018). In Wonosobo's highlands, such strategies may be essential to counteract harsh microclimatic conditions and prevent the further dominance of decomposers under warmer and more variable climates.

The findings from Wonosobo highlight several research priorities needed to build a comprehensive resilience framework for tropical mountain agroecosystems. First, seasonal and multi-year monitoring of insect assemblages is essential to capture temporal dynamics influenced by cropping cycles, climate fluctuations, and pest outbreaks—factors often overlooked in short-term studies. Second, functional trait analyses (e.g., body size, dispersal potential, thermal thresholds) would refine understanding of species' responses to microclimatic gradients and inform predictive models of future community shifts. Third, integration of soil microbial and invertebrate communities is needed to complement aboveground insect data and clarify nutrient cycling pathways, especially in manure-intensive highlands. Fourth, landscape-level spatial modeling could identify ecological corridors, invasion gateways, and microclimatic refugia that support biodiversity and regulate species dispersal. Fifth, socioecological studies focusing on farmer practices, knowledge transfer, and adoption barriers would ensure that ecological recommendations align with local livelihoods and policy realities. Collectively, these research directions contribute to a holistic framework that integrates ecological, climatic, and social dimensions to support long-term resilience in Wonosobo and similar tropical mountain systems globally.

In conclusion, insect diversity in Wonosobo's agricultural gradient is strongly shaped by altitude, microclimate, and land-use structure, producing distinct ecological patterns across lowland, mid-elevation, and highland farms. Diversity metrics highlight these contrasts: species richness and Margalef richness peak in Blederan (S = 27; DMg = 4.99), while Shannon diversity remains high in both Blederan (H′ = 2.25) and Karangsambung (H′ = 2.45). Evenness is highest in the lowlands (E = 0.76), indicating stable abundance distributions, whereas Sembungan shows reduced richness (S = 17), lower diversity (H′ = 2.03), and higher dominance (C = 0.176), reflecting strong environmental filtering and the numerical dominance of *M. domestica* and *L. simplex*. Functional guilds further reinforce these gradient-wide patterns: lowland and mid-elevation systems host balanced assemblages of herbivores, predators, nectarivores, and detritivores, while high-elevation farms collapse into decomposer-dominated networks with minimal redundancy. These shifts elevate invasiveness risks at ecological extremes, particularly in Sembungan where manure-based fertilization and harsh microclimates promote synanthropic Diptera. The integration of ecological indices, trophic structure, and invasiveness dynamics shows that mid-elevation mosaics serve as the most resilient agroecosystems, whereas highlands are the most vulnerable. Enhancing vegetation heterogeneity, improving microclimate buffering, and strengthening biological control are therefore critical strategies to sustain biodiversity and ecosystem services in Wonosobo's tropical mountain agriculture.

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